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Forecasting the global extent of invasion of the cereal pest *Spodoptera frugiperda*, the fall armyworm

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Abstract

Fall armyworm, *Spodoptera frugiperda*, is a crop pest native to the Americas, which has invaded and spread throughout sub-Saharan Africa within two years. Recent estimates of 20–50% maize yield loss in Africa suggest severe impact on livelihoods. Fall armyworm is still infilling its potential range in Africa and could spread to other continents. In order to understand fall armyworm's year-round, global, potential distribution, we used evidence of the effects of temperature and precipitation on fall armyworm life-history, combined with data on native and African distributions to construct Species Distribution Models (SDMs). We also investigated the strength of trade and transportation pathways that could carry fall armyworm beyond Africa. Up till now, fall armyworm has only invaded areas that have a climate similar to the native distribution, validating the use of climatic SDMs. The strongest climatic limits on fall armyworm's year-round distribution are the coldest annual temperature and the amount of rain in the wet season. Much of sub-Saharan Africa can host year-round fall armyworm populations, but the likelihoods of colonising North Africa and seasonal migrations into Europe are hard to predict. South and Southeast Asia and Australia have climate conditions that would permit fall armyworm to invade. Current trade and transportation routes reveal Australia, China, India, Indonesia, Malaysia, Philippines and Thailand face high threat of fall armyworm invasions originating from Africa.

Keywords

Agriculture, biological invasion, climate envelope, crop pest, ecological niche model

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Introduction

Fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is native to the Americas. The moth lives year-round from as far south as La Pampa, Argentina, to as far north as southern Florida and Texas, USA and undergoes seasonal migrations as far north as Québec and Ontario (Figure 1). Fall armyworm caterpillars are major pests of cereals and forage grasses and are recorded as eating 186 plant species from 42 families (Casmuz Augusto 2010). Fall armyworm is one of the most serious pests of maize in the America. Yield losses can reach 40% in Honduras (Wyckhuys and O'Neil 2006) and 72% in Argentina (Murúa et al. 2006). In addition to maize, fall armyworm attacks many other economically important, e.g. rice, sugarcane, sorghum, beet, tomato, potato, cotton and pasture grasses (Abrahams et al. 2017; Day et al. 2017). Therefore fall armyworm could pose a risk to subsistence and cash crops in large parts of the world.

In January 2016, major outbreaks of armyworms were reported in South West Nigeria and Ghana and shortly after in Benin, Sao Tomé and Togo (International Institute of Tropical Agriculture 2016). Morphological and molecular analysis confirmed that the armyworms were *S. frugiperda* and not the native armyworms *S. exigua* or *exempta* (CGIAR 2016). As of 28 September 2017, 28 sub-Saharan African countries had confirmed the presence of fall armyworm, with nine more suspecting or awaiting confirmation of the species' presence (Abrahams et al. 2017). Within these countries the fall armyworm is still spreading (Njeru 2017). The countries of the initial outbreaks (Ghana, Benin, Togo and Nigeria) have West Africa's major air transportation hubs and have similar warm, moist climates to the regions from which many arriving flights originate (Chapman et al. 2017; Tatem 2009). As a result, this region is particularly likely to act as an epicentre for invasions in Africa (Early et al. 2016). Indeed, it is speculated that fall armyworm entered Africa as a stowaway on a passenger flight (Cock et al. 2017); unaided dispersal is considered unlikely because prevailing winds are generally from East to West. Molecular data from specimens in Togo indicate that fall armyworm in Africa originates from an area encompassing the eastern USA, Caribbean and Lesser Antilles (Nagoshi et al. 2017). The two known strains of the species, the so-called maize- and rice strains, overlap in the latter region and both strains have been found in Africa (Cock et al. 2017, Nagoshi et al. 2017). However, it is still unclear whether the invasion originated from single or multiple introductions. Differences in host plant and mating time between the strains (Hänniger et al. 2017) suggest it is unlikely that both strains would have been introduced separately. The rapid spread throughout Africa was possibly aided by intra-continental transportation links (Faulkner et al. 2017). However, the ability of adult fall armyworm moths to travel very long distances was probably the major factor. Adults can travel several hundred kilometres in a single night by flying to and maintaining an elevation of several hundred metres, at which height winds can transport them in a directional manner (Westbrook et al. 2016).

Fall armyworm's year-round distribution is expected to be restricted to relatively warm and moist areas, as it cannot survive cold temperatures by entering diapause (Nagoshi et al. 2012). However, fall armyworm poses a threat outside its year-round range,
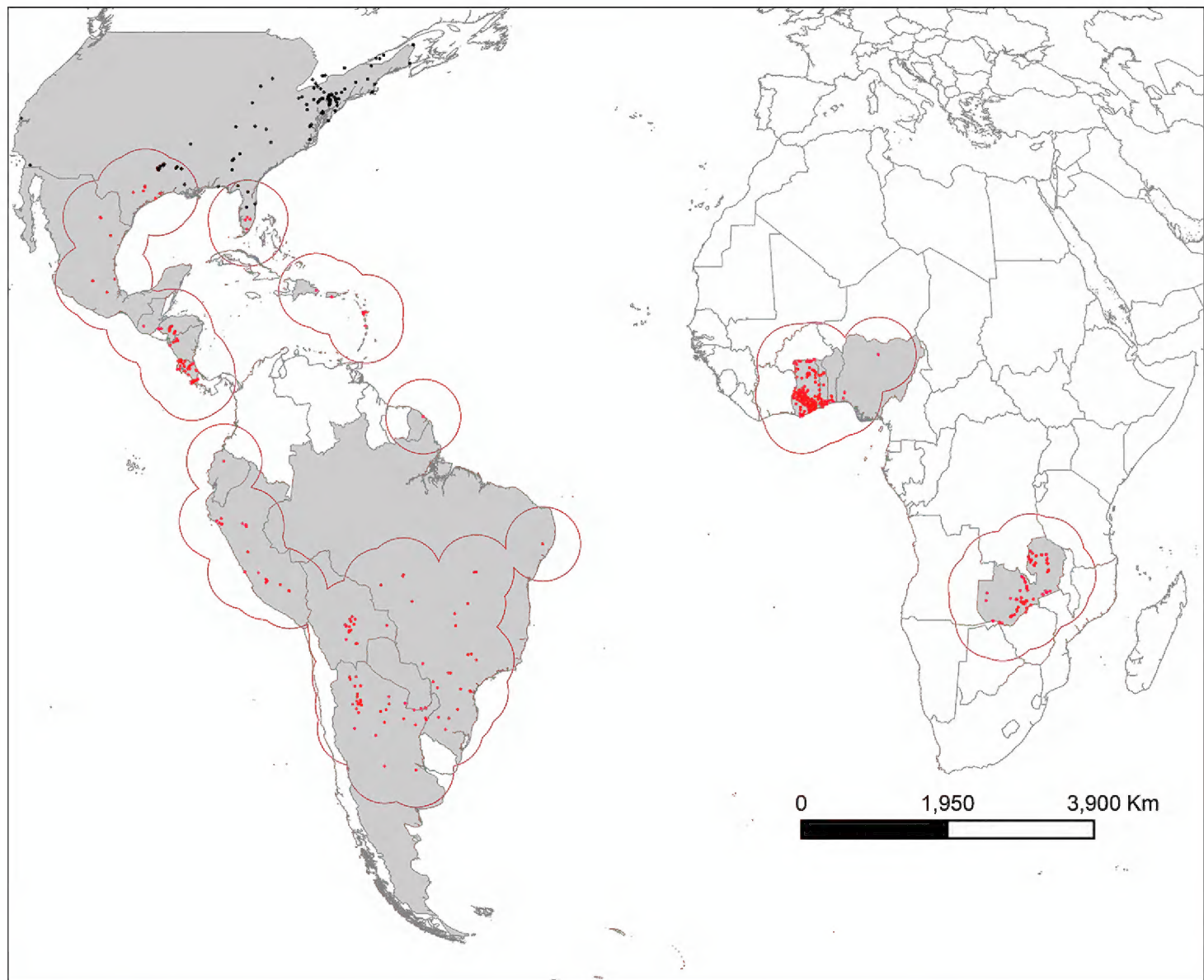
Figure 1. Fall armyworm distribution data. Red points are the complete set of presence locations used to make models. Black points in the USA are not part of the year-round native distribution and were not included in models. Grey areas are the geographically unrestricted background from which pseudo-absences could be drawn. Red lines indicate the geographically restricted background (500 km radius around presence locations) within which pseudo-absences could be drawn.

including in temperate regions, because it undergoes very long distance seasonal migrations. Between spring and autumn, three successive generations of fall armyworm travel 1700 km north from Texas and Florida to infest crops as far north as Québec and Ontario (Westbrook et al. 2016). Adults also appear to migrate several hundred kilometres over the sea (Westbrook et al. 2016). This means that North African countries could be within the reach of fall armyworm from sub-Saharan populations. If the species can survive year-round in North Africa, then seasonal migrations into Europe could also occur. This would pose a severe threat to agriculture in Europe, where the species is classed as a Quarantine Pest by the EU (Efsa Panel on Plant Health et al. 2017). Further afield, the fall armyworm's wide distribution in the Americas and Africa suggest that it could establish easily in East and Southeast Asia. Given increasing levels of trade and transportation between infested parts of Africa and the rest of the world (Chapman et al. 2017), it seems likely that fall armyworm could be unwittingly transported onwards to environmentally suitable regions.

As fall armyworm has huge potential to affect staple and economic crops globally, we urgently need information on the pest's potential distribution and environmental limitations. Such information would assist national and regional pest risk assessments and appropriate management strategies in several ways: by quantifying the agricultural areas within Africa that are at risk from year-round populations or seasonal migrations, by informing the likelihood of seasonal migrations outside Africa, and by classifying the likelihood of establishment if fall armyworm is transported into other parts of the world. This information would also help target awareness raising and monitoring for early detection. Early detection of infestations is extremely beneficial as chemical insecticides are only effective while the larvae are small (Bessin 2003). Early-stage larvae live inside the whorl of the developing plant and so are hard to detect with casual observation. Detecting fall armyworm in time to apply pesticide and avoid heavy crop losses means inspecting plants for eggs or larvae or setting pheromone traps for adults (Njeru 2017). Raising awareness amongst farmers and developing surveillance schemes is therefore a priority for managers (Njeru 2017). Knowing where outbreaks are likely to occur would encourage and inform these efforts.

Here, we first reviewed what is known of the environmental controls on the fall armyworm's life-cycle and herbivory, particularly on maize, the crop most economically important and threatened by the moth in Africa (Njeru 2017). We then quantified the species' environmental controls and potential distribution worldwide, using information on the native and invasive distributions to construct an ensemble SDM. SDMs find statistical correlations between species' distributions and environmental factors and ensembling results from multiple SDM types identifies areas that techniques agree are highly suitable for the species. We assessed the robustness of the SDM approach by asking whether fall armyworm has invaded parts of Africa, not predicted by a climatic SDM, i.e. undergone a 'niche shift' (Early and Sax 2014). The SDMs we constructed are based on annual environmental conditions and thus predict suitability for year-round populations of fall armyworm. Lastly, we use trade and transportation links to interpret the potential for the fall armyworm to spread beyond Africa via these pathways.

Methods

Effect of abiotic and host plant characteristics on life-cycle

To forecast a species' potential range, it is necessary to consider the environmental factors that are needed for the species to complete its life cycle. These factors could directly limit the target species' distribution and are often termed 'proximal' variables. Using these variables increase accuracy and biological realism of projections of species distributions following invasion (also termed 'transferability'(Petitpierre et al. 2017)). We reviewed the literature of field observations and experimental studies into fall armyworm to investigate the linkages between the environment and life cycle (Figure 2, Suppl. material 1: Table S1). The studies were conducted on different populations and
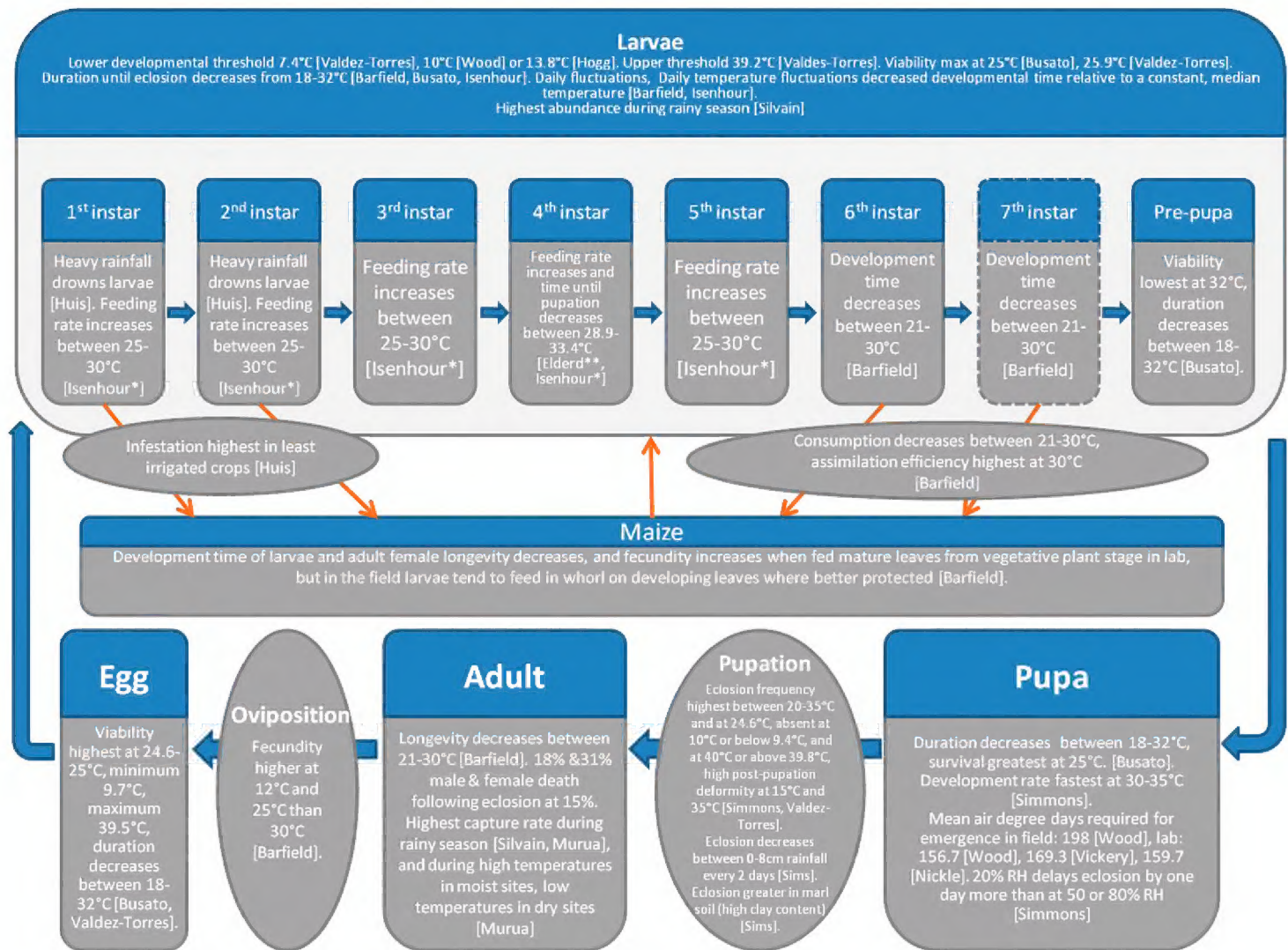
Figure 2. Empirically measured environmental effects on fall armyworm life cycle. Summary of data from literature of temperature, moisture, soil and host plant effects on fall armyworm survival and developmental time and observations of abundances in the field under different conditions and seasons. All studies were conducted with populations from the Americas. Rectangles are life stages, ovals are processes. Orange arrows represent effects of fall armyworm on maize or vice versa. The occurrence of a 7th instar is not universally reported. Only direct effects (measured or imputed) of the environment and host on fall armyworm were included. Unless otherwise noted, moths for experiments were reared on fresh maize or an artificial diet. RH is relative humidity. More information is given in Suppl. material 1: Table S1, Figure S5

the population's strain (which could affect physiology, see below) was rarely reported. Nonetheless, informative patterns emerged. We summarise the patterns below and in Figure 2, but full details and references are in Suppl. material 1: Table S1.

Environmental data

Based on the life-history and environmental requirements of fall armyworm, and in light of climatic conditions in the Americas and Africa, we selected the following climatic variables:

– SumWet, total amount of precipitation in wettest three months of year (intensity of rainy season, when most food available and population growth is fastest)

– LenWet, number of months when rain is greater than average (length of rainy season, when most food is available and population growth is fastest)
– SeasPpn, seasonality of precipitation (difference in rainfall between rainy and dry season)
– MinTemp, mean temperature of the coldest month of the year (the lowest limit for growth)

We also initially used GDD13.8, annual growing degree days above a lower development threshold of 13.8 °C (minimum temperature for survival). We selected 13.8 °C as the lower development threshold (Hogg et al. 1982), as this value is widely cited by other researchers. However, the correlation between MinTemp and GDD13.8 is 0.98. This degree of collinearity can cause inaccurate measurement of the relationship between the explanatory and response variables (Dormann et al. 2012). We removed GDD13.8, as MinTemp has the more intuitive link with species distributions and a clear temperature threshold for fall armyworm survival is widely reported (Suppl. material 1: Table S1). Indeed, fall armyworm populations in west Argentina occur in areas with substantially fewer growing degree days than the populations in the USA. This suggests that the cold range margin is more likely to be set by MinTemp than GDD. No other environmental variables had a collinearity greater than 0.7, which is considered an acceptable threshold (Dormann et al. 2012). There is considerable variation in the rainy season between America and other parts of the world, particularly Africa (Leff et al. 2004). The precipitation variables were therefore chosen to accommodate variation in the timing and length of the rainy season or even multiple rainy seasons (e.g. West vs. East Africa). Climatic variables were calculated from monthly averages for the period 1961–1990, derived from the climatic research unit (CRU) dataset at 10 arc-minute resolution (New et al. 2002).

In addition to climatic variables, we also used 'Forest', the proportion of each 10 arc-minute grid-cell that is covered by trees. This is because fall armyworm is only reported from agricultural areas, though there may be many areas covered by forest that are climatically suitable for the species, but from which it is not reported or is absent due to a lack of host plant. We therefore expected a high forest cover to indicate environmental unsuitability. Without the forest variable, climate conditions alone would have been less able to discriminate between suitable and unsuitable locations. We used forest rather than crop or pasture land as forest is relatively easier to delineate than grassland using satellite data. Forest cover was drawn from the European Space Agency's Global Land Cover 2000 project at 1 km (https://www.esa-landcover-cci.org/).

Distribution data

Presence records for the Americas were obtained from three sources. 1) Global Biodiversity Information Facility (ww.gbif.org) in November 2016. Records that did not have coordinates but did have location descriptions were georeferenced with accuracy equal to the climatic grid data. 2) Review of literature on Fall Armyworm in the region.

3) Consultation between CABI and local experts in several countries. In the southern USA, occurrences south of 27 degrees in Florida and south of 31 degrees in Texas were considered to be year-round populations and were included as presence data points (Westbrook et al. 2016). Other USA populations were not included as they represent seasonal migratory populations. In total, 876 presence locations were found. Data and sources for the Americas that can be shared publicly are available in Suppl. material 2: Table S2. Distribution data for Africa were obtained from four sources. 1) A survey of farming households in Ghana and Zambia, conducted in July 2017 (Abrahams et al. 2017). The countries were stratified into geographic regions, within which survey locations were chosen randomly. Surveys yielded 466 incidences of farming households observing symptoms or larvae of fall armyworm in their fields. 2) Published literature (Goergen et al. 2016; Nagoshi et al. 2017). 3) Infestations of fall armyworm reported to CABI's Plantwise clinics in Ghana and Zambia from July 2016–June 2017. 4) Seven pheromone traps in Ghana managed by the USAID Agricultural Development and Value Chain Enhancement (ADVANCE) project, from April 2017–July 2017.

Distribution data were filtered so that only one presence was recorded in each climatic grid-cell, resulting in 240 presences in Africa and 167 presences in the Americas. Due to the recent dedicated searches, the African distribution was better sampled than the American distribution. The difference in sampling intensity between the two continents led to concerns that SDMs might be over-fitted to the well-studied locations in Ghana and Zambia. This would underestimate the suitability of areas outside Ghana and Zambia, particularly areas that are environmentally similar to the native range, but different to the Ghanaian and Zambian range. We therefore sub-sampled several proportions of the African distribution (5, 10, 20, 30, 50 and 70%) and used four sub-samples at each proportion to construct alternative SDMs.

In order to select pseudo-absences, we used two approaches to delimit the geographic background in the Americas and Africa to which fall armyworm could reasonably be expected to disperse without human assistance (Figure 2, VanDerWal et al. 2009). First, we used all countries in America and Africa in which fall armyworm records were available. American countries were excluded from the backgrounds if they did not have records of fall armyworm but (i) fall armyworm is known to be present (determined using CABI's Crop Protection Compendium, https://www.cabi.org/cpc/about/ and internet searches) or (ii) if the country is surrounded by countries in which fall armyworm is recorded. This exclusion avoided the inclusion of countries in the background where the species is present but had not been sampled, reducing the probability of 'false absences'. Second, we investigated the impacts of restricting the geographic background to the region within 500 km of presence points (Figure 1). Specifying an upper distance can help prevent models from contrasting completely different climate conditions, e.g. temperate vs. tropical (VanDerWal et al. 2009). This contrast would only yield the information that fall armyworm can live in the tropics all year round. For both approaches, pseudo-absences were randomly placed in climatic grid-cells within the background region, but outside occupied grid-cells. The placement of pseudo-absences was repeated 20 times for each sub-sample. In each distribu-

tion dataset, the number of pseudo-absences was the same as the number of presences used (i.e. prevalence was always 0.5).

In total, we ran models with 488 datasets: six different levels of sub-sampling of African presences from the entire background (5, 10, 20, 30, 50 and 70%) each with 20 repetitions of sub-sampling, one dataset of all presences using the entire background, and one dataset with the geographically restricted background and for each of which we randomly sampled pseudo-absences four times.

Species distribution modelling

In order to estimate parameter values for the environmental variables, and to predict the potential year-round distribution of fall armyworm, we created an ensemble SDM (Araújo and New 2007). The ensemble included eight modelling techniques: artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalised additive models (GAM), generalised linear models (GLM), multivariate adaptive regression splines (MARS), random forest (RF) and surface range envelope (SRE, note this does not use pseudo-absence data in model calibration but does in validation). Analyses were undertaken in R (R Core Team 2016) using the biomod2 package (Thuiller et al. 2014) and default SDM settings.

We used internal validation to evaluate SDM accuracy, splitting each of the 488 distribution datasets randomly so that 70% of the presence and pseudo-absence points were used to calibrate the models. These models were used to predict suitability at the 30% remaining validation distribution data points. The Area under the Receiver Operating Curve (AUC) and True Skill Statistic (TSS) were used to judge how accurately the models predicted the validation data (Lawson et al. 2014).

For each of the distribution datasets, we constructed an ensemble forecast for the global terrestrial surface. Ensembles were made using models (from the 488 distribution datasets) for which validation TSS ≥ 0.4. Models with TSS ≥ 0.4 are considered to have 'moderate' performance (greater than 'fair', but less than 'substantial' (Landis and Koch 1977)). However, we used all presence and pseudo-absence points in the given dataset to construct the final models to be included in the ensemble (i.e. not just the 70% of the data used in calibration). This was to ensure that, when a combination of dataset and technique yielded moderate accuracy, all of the data in that dataset were then used to maximise the information in the final model. In order to be confident that TSS and AUCs of the internally validated models reflected the accuracy of the full models used to project distributions, we calculated the Spearman's correlation between global projections from internally validated and full models. To construct ensembles, the selected models were rescaled so that projections were on the same numerical scale and the mean suitability predicted by all retained models was calculated, weighted by the accuracy (TSS) of each model. This method has been shown to be the most accurate of the 'traditional' ensembling methods that could be applied to these data (Gritti et al. 2013).

In order to investigate the effect of biased recorder effort and geographic background on environmental suitability, we compared the agreement of the global ensemble projections made using each distribution dataset by using Cohen's Kappa and balanced accuracy (Brodersen et al. 2010). For the latter, we binned projected suitabilities into 20 percentile bins and calculated how well the projections from one dataset classified the projections from another dataset.

In order to determine whether the environment in the geographic region from which distribution data were drawn is representative of the entire global terrestrial surface, we calculated the Multivariate Environmental Similarity Surface (Elith et al. 2010; Hijmans et al. 2012). If there are environmental conditions somewhere in the world that have "no analogue" with environmental conditions in the American and African backgrounds, SDM projections into these regions would be extrapolations, with added uncertainty.

The importance of environmental variables for fall armyworm's range was calculated using all of the distribution data in a given dataset and using all models, regardless of TSS score. For any given environmental variable, that variable was randomised, an SDM was made with the shuffled dataset and the Pearson's correlation (r) calculated between the SDMs with original and shuffled data. Importance is calculated as 1-r, so a value 0 indicates the variable has no influence on the SDM.

Has the fall armyworm invaded where we expect it to, based on the native distribution in the Americas?

To answer this, we calculated the niche expansion between the Americas and Africa, using the methodology developed by Broennimann et al. (2012). The environment (climate and forest cover) in the two regions is decomposed into the most important trends using a Principal Components Analysis (PCA). We used all distribution data from the native year-round range and from the studied African range in Figure 1 (i.e. there was no sub-sampling). We then divided this environmental space into a grid of 100 × 100 cells. We measured the density of species occurrences for each combination of environmental conditions in each grid-cell of the environmental space using a kernel smoother function to correct for sampling bias and environmental availability and to ensure that the results were independent of the grid resolution. These analyses were done using ecospat package (Di Cola et al. 2017) in R v3.4.1 (R Development Core Team 2017) . We used these gridded data to calculate how much of the African niche remained within the native niche ('niche stability'). Niche stability is the proportion of the densities in the colonised range that overlaps with the native range.

Transportation beyond Africa

In order to illustrate the potential for fall armyworm to spread from Africa to other parts of the world, we first identified the countries most likely to act as sources for fall armyworm and the countries most vulnerable to fall armyworm establishment, as

those with > 33660 km² of suitable climate (i.e. 100 × 10 arc-minute grid-cells with climate suitability > 0.5). This resulted in 64 countries being identified as sources or vulnerable. We then examined two major pathways for invertebrate introduction: trade and passenger air travel. Trade is one of the main drivers of plant pest introduction globally (Chapman et al. 2017). We used values of all traded goods, as the propensity of fall armyworm to be transported with particular commodity types is not yet known, and all trade provides a reasonable estimate of introduction likelihood for a range of species (Seebens et al. 2015). We obtained United Nations data on total exports from sub-Saharan African countries to all countries for the period 2012–2016 (2017 data appeared to be too incomplete to use). Data were obtained from the UN Comtrade database (https://comtrade.un.org/). We considered the trade routes most likely to transport fall armyworm as those with a total trade volume > 500,000,000 USD during the reporting period (the top 5% of trade routes from source to vulnerable countries).

Passenger air travel is suggested to be the route by which fall armyworm was first introduced to Africa and is thought to be important in insect introductions (Tatem and Hay 2007). Of 725,000 interceptions of plant pests (largely insects) in the US, 62% of intercepted pests were associated with baggage (McCullough et al. 2006). We used data on the number of passengers in 2013 whose embarkation point is in a sub-Saharan African country and whose final destination is outside sub-Saharan Africa. Data were obtained from the VBD-Air tool (Huang et al. 2012). We considered the country to country air travel routes most likely to transport fall armyworm as those that carry > 10000 passengers during the reporting period (the top 13% of air travel routes from source to vulnerable countries). We then mapped the trade and air travel routes from source countries in sub-Saharan Africa to vulnerable countries worldwide.

Results

Effect of abiotic and host plant characteristics on life-cycle

The most commonly studied relationship between life-history stage and environment is the effect of air temperature on larval and pupal survival and development rates. The minimum temperature for development was reported between 8.7 °C and 13.8 °C (Busato et al. 2005; Hogg et al. 1982; Valdez-Torres et al. 2012; Wood et al. 1979). Several studies found evidence that the developmental time of egg, larval, pre-pupal and pupal stages decreases with temperature up until 32–33.5 °C (or even 35 °C) (Barfield and Ashley 1987; Busato et al. 2005; Elderd and Reilly 2014; Hogg et al. 1982; J. Isenhour et al. 1985; Simmons 1993). However survival of these stages is greatest around 25 °C (between 20 and 32 °C), and 35 °C appears to be an upper limit on survival (Barfield and Ashley 1987; Busato et al. 2005; Simmons 1993; Valdez-Torres et al. 2012). Fecundity and adult longevity is greatest between 21 and 25 °C (Barfield and Ashley 1987). Constant temperatures do not represent real conditions in the field and studying the effects of fluctuations can be informative. When median temperatures are between 15 and 25 °C,

daily fluctuations above and below these temperatures increase pupal and larval development rates and decrease adult deformity (Barfield and Ashley 1987; Simmons 1993).

The importance of moisture and precipitation is complex. Precipitation and irrigation have a direct negative effect on larval and pupal survival. Heavy rainfall fills the maize whorl with water, in which larvae float, until it overflows and the larvae are spilled out or drown (a process which is helped by wind gusts, A. van Huis 1981). Rainfall and irrigation are thought to trap moths and drown them in their pupation tunnels, with the effects being stronger in more friable soils, when rainfall can also cause the tunnels to collapse (Sims 2008). In fact, a local control measurement in Zambia involves spreading ashes in the funnel in order to exacerbate the effect of water (pers. comm. Patrick Kalama). Lack of moisture during pupal stages appears to have little direct effect on survival or development rates (Simmons 1993). However, indirect effects of moisture are likely more important for fall armyworm population sizes than direct effects. This is because abundance tends to peak during rainy seasons, particularly in drier sites, possibly because of increased host plant growth (Murúa et al. 2006; Silvain and Ti-A-Hing 1985). On the other hand, infestation rates are highest in maize deprived of irrigation for the longest, likely because plant moisture stress favours insect development (van Huis 1981).

Research on the effect of host plant on fall armyworm populations is limited to maize. There is evidence that the maize growth stage positively impacts development speeds (i.e. development is fastest for larvae eating mature leaves) (Barfield and Ashley 1987). This is unexpected, as leaf nutritional value typically declines with growth stage. It is unclear whether this finding is relevant to field populations, as larvae prefer to feed in whorls on developing leaves, presumably for protection (Chapman et al. 1999).

There are two genetically distinct fall armyworm 'strains', which specialise on maize and rice (Nagoshi et al. 2007). Some inter-strain mating can occur; rice strain females prefer to accept maize strain males, resulting in mixed populations, but maize strain females and rice strain males appear to be reproductively incompatible (Hardke et al. 2015). Both strains appear to be present in Africa (Cock et al. 2017; Nagoshi et al. 2017). The strains differ in the rates of larval development on the host plants, mating behaviour, use of food resources, resistance to insecticides and variation in susceptibility to plants expressing *Bacillus thuringiensis* (Bt) proteins (Hardke et al. 2015; Nagoshi et al. 2017). There is evidence for variation in the environmental tolerances of the two strains. Basal temperature was found to be 10.6 °C and 10.9 °C for two populations of the maize strain and 9.5 °C and 9.6 °C for two populations of the rice strain (though no statistical test was done, Busato et al. 2005) and seasonal abundance varies differently for the two strains in Florida (Nagoshi and Meagher 2004). There is therefore an argument for constructing separate SDMs for each strain, but the distributions and inter-breeding status of the two strains are not sufficiently known to do this and we therefore treat the strains as a single entity.

Has the fall armyworm invaded where we expect it to, based on the native distribution in the Americas?

All but 3% of the recorded current distribution in Ghana and Zambia is found in climate and forest conditions that match the native range, i.e. there is virtually no
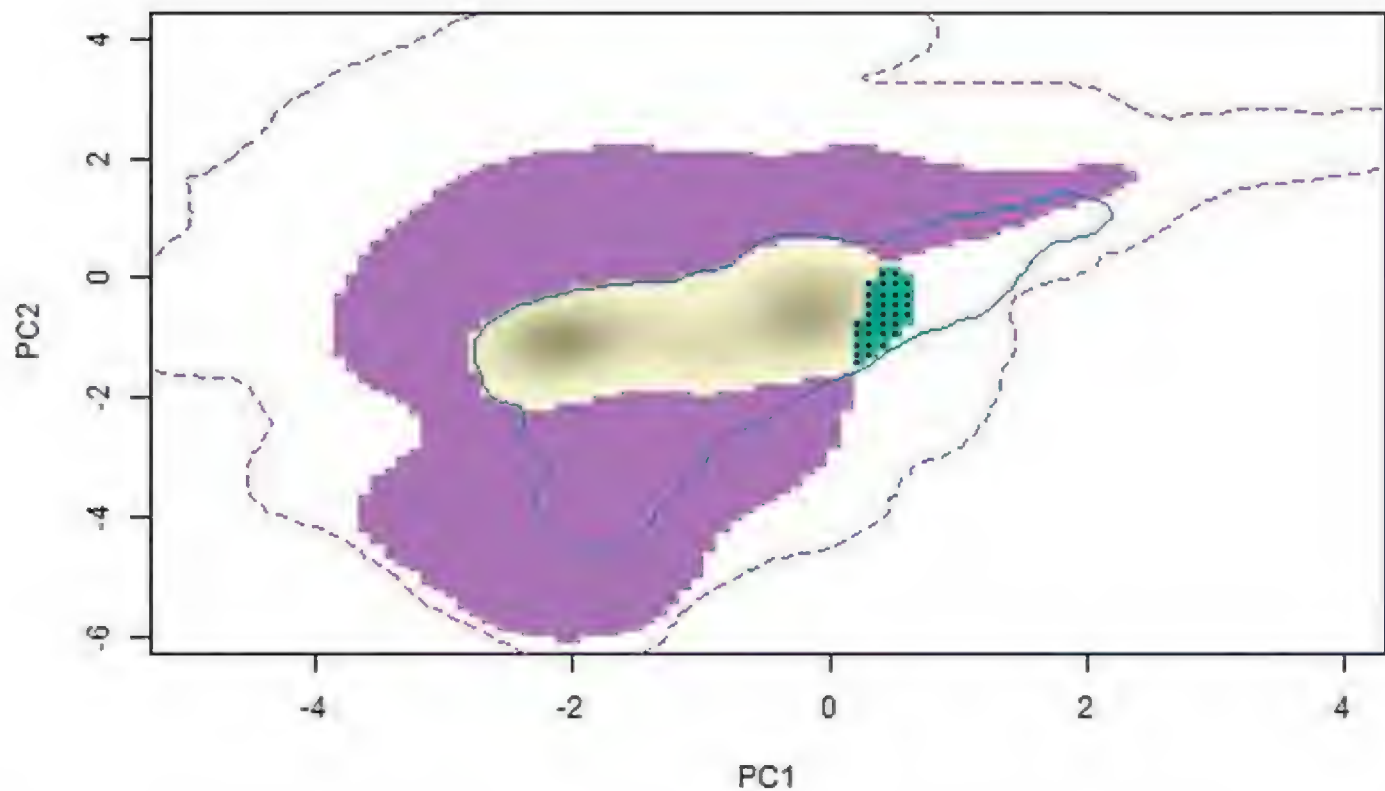
Figure 3. Similarity of environmental niches in the Americas and Africa. The outlines represent the environmental conditions available in the Americas (purple, solid line) and Ghana and Zambia (green, dashed). The larger purple shaded area represents the conditions the species occupies only in the Americas. The yellow shaded areas represent the conditions the species occupies in the studied African range that lie within the American environmental niche (niche stability). The green area with dots shows the part of the African range that is found in different environmental conditions to the native range (niche expansion). The shading under the yellow/green area is the density of the species' occurrence in the African range.

orange area in Figure 3. Fall armyworm therefore does not appear to have undergone niche shift during invasion.

SDM performance

Internal cross-validation indicated that TSS scores were 'moderate' and AUC scores were 'fair' (Table 1). These scores increased as more of the African distribution data were included in analyses. The Spearman correlations between global projections made using the validation data (70% of each distribution data set) and all data in each distribution dataset were ≥ 0.87. This indicates that the TSS and AUC scores from internal validation reflect the accuracy of SDMs calculated with all data in each dataset.

Agreement between the ensemble projections resulting from sub-sampled and complete datasets was 'moderate' to 'substantial' (Cohen's kappa values Table 1, Suppl. material 1: Figure S1). Agreement increased with the percentage of the African data sub-sampled (Suppl. material 1: Figure S2). Ensemble projections from different datasets agreed most strongly in the areas that are least suitable, i.e. < 0.2 (Suppl. material 1: Figure S2). The proportion of grid-cells classified within the same suitability band ('balanced accu-

Table 1. Summary statistics for Species Distribution Models (SDMs). 'Dataset' indicates the percentage of the African distribution data that were sub-sampled. AUC and TSS indicate predictive accuracy. Mean (±standard deviation) TSS and AUC values are averages calculated by internal cross-validation for all SDMs constructed with each dataset, excluding SDMs that were discarded in making the ensemble due to low predictive accuracy (TSS <0.4). TSS values between 0.4 and 0.5 are often considered 'moderate'(Landis and Koch 1977). AUC values between 0.7 and 0.8 are often considered "fair". Spearman's ρ is calculated between the global ensemble projections made using 70% (used for internal cross-validation) and 100% of the data and indicates whether the validation statistics can be considered representative of the final model. Cohen's Kappa measures the agreement between the global ensemble forecast using 100% of the distribution data and the entire background and the named dataset. Kappa values of 0.4–0.6 are considered 'moderate', and 0.6–0.8 'substantial'(Landis and Koch 1977).

Pseudo-absence restriction radius	Dataset	TSS	AUC	Spearman's ρ	Cohen's Kappa
None	5%	0.52±0.06	0.79±0.05	0.88±0.12	0.49
None	10%	0.52±0.07	0.80±0.05	0.87±0.15	0.50
None	20%	0.54±0.09	0.80±0.06	0.89±0.09	0.57
None	30%	0.55±0.06	0.80±0.04	0.87±0.12	0.59
None	50%	0.51±0.07	0.79±0.05	0.89±0.11	0.75
None	70%	0.55±0.07	0.91±0.05	0.91±0.09	0.76
None	100%	0.55±0.07	0.81±0.06	0.89±0.08	NA
500 km	100%	0.48±0.07	0.78±0.04	0.79±0.23	0.41

racy') by different ensembles was never less than 0.6 when pseudo-absences were selected from the entire geographic background. Balanced accuracy and increased between ensembles constructed with similar degrees of sub-sampling (Suppl. material 1: Figure S2).

The dataset using 100% of the data and the entire geographic background gave SDMs that had the highest AUC and TSS scores (Table 1). There was very little difference in the shape or extent of the area in the native American region predicted to be suitable using different sub-samples of the distribution data (Suppl. material 1: Figure S1). This and the high degree of agreement in the global projections from SDMs using all and sub-sampled African data (Suppl. material 1: Figures S1, S2), suggest that SDMs using 100% of the data did not appear to be over-fit to the African distribution data. SDMs constructed using pseudo-absences drawn from a 500 m buffer around presence points (Figure 4) appeared to under-predict both the American and African distribution (Suppl. material 1: Figure S1) and had the lowest TSS and AUC scores (Table 1). We therefore saw no reason not to use predictions from SDMs using the complete distribution dataset and the entire geographic background to represent fall armyworm's global potential distribution. These SDMs were used in the final ensemble global projection (Figure 4).

MinTemp was the most important environmental variable, followed by forest and SumWet (Figure 5). SeasPpn and LenWet were relatively unimportant. Fall armyworm was most commonly found in areas with very little forest cover, a minimum annual temperature of 18–26 °C and with 500–700 mm rainfall in the three wettest months (Suppl. material 1: Figure S3). The degree of sub-sampling did not affect variable importance. The range of the environmental conditions from which fall armyworm is recorded is shown in Suppl. material 1: Figure S3.
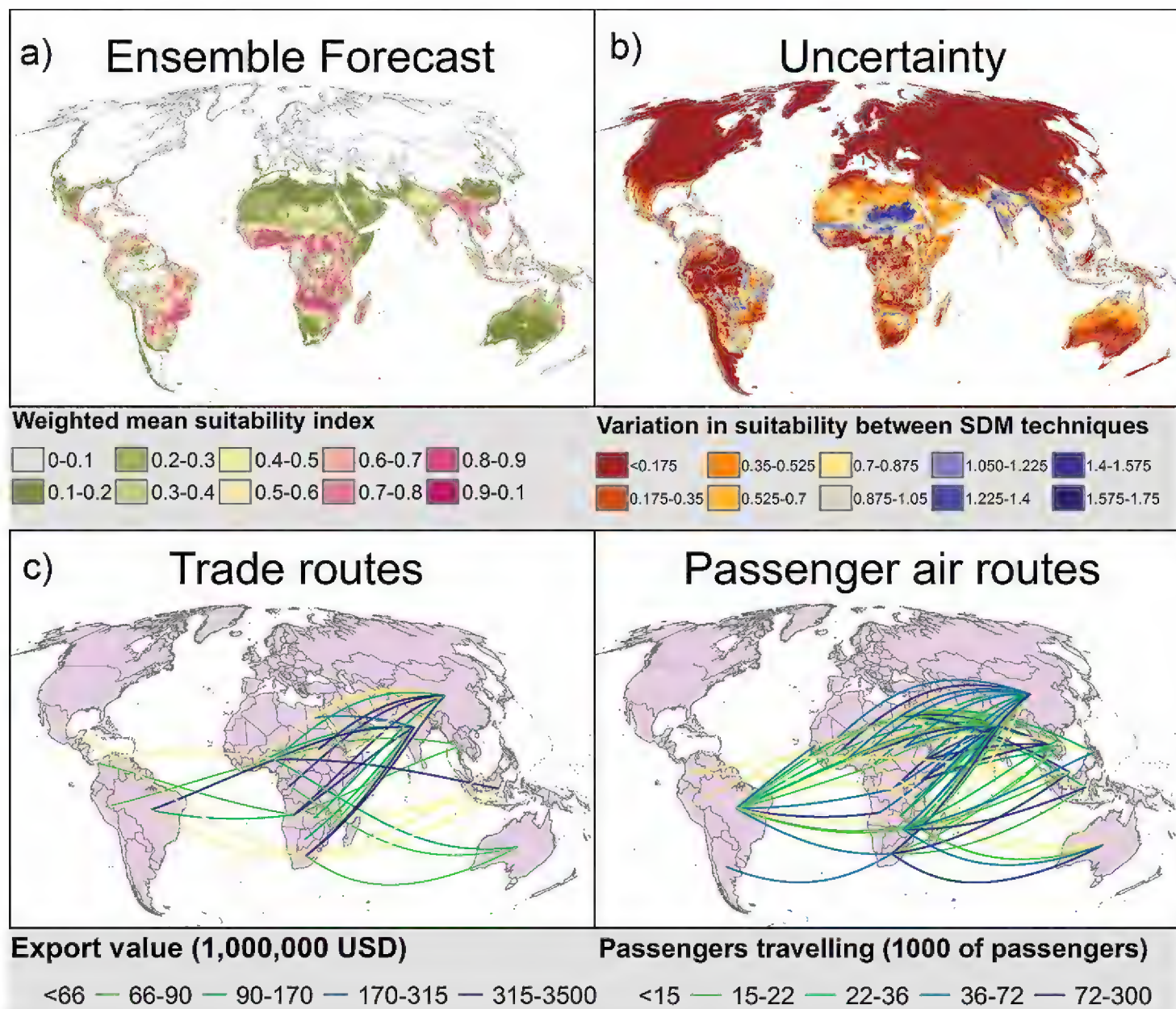
Figure 4. Global suitability for fall armyworm and likely invasion routes. **a** Potential global distribution of fall armyworm, as predicted by an ensemble of SDMs constructed using all distribution data and with four pseudo-absence datasets. SDMs were permitted into the ensemble if the TSS from internal cross-validation was ≥0.4. The ensemble was calculated as the mean of projections from all permitted SDMs, each model weighted by the cross-validated TSS **b** uncertainty in projections, as calculated by the variation between all projections included in the ensemble **c** value of all exports from 2012–2016 from source sub-Saharan African countries climate to vulnerable countries outside sub-Saharan Africa. The top 5% of trading relationships between these countries are shown and the five colour categories represent 20% quantiles of export values **d** number of passengers in 2013 travelling from source sub-Saharan African countries with their final destination in vulnerable countries outside sub-Saharan Africa. The top 13% of travel routes between these countries are shown and the five colour categories represent 20% quantiles of passenger numbers.

MESS indicated very few areas in which environmental conditions had no analogue in the training region (Suppl. material 1: Figure S4).

Transportation beyond Africa

Countries vulnerable to fall armyworm (outside South America) that receive the greatest value of commodities exported from African fall armyworm source countries are
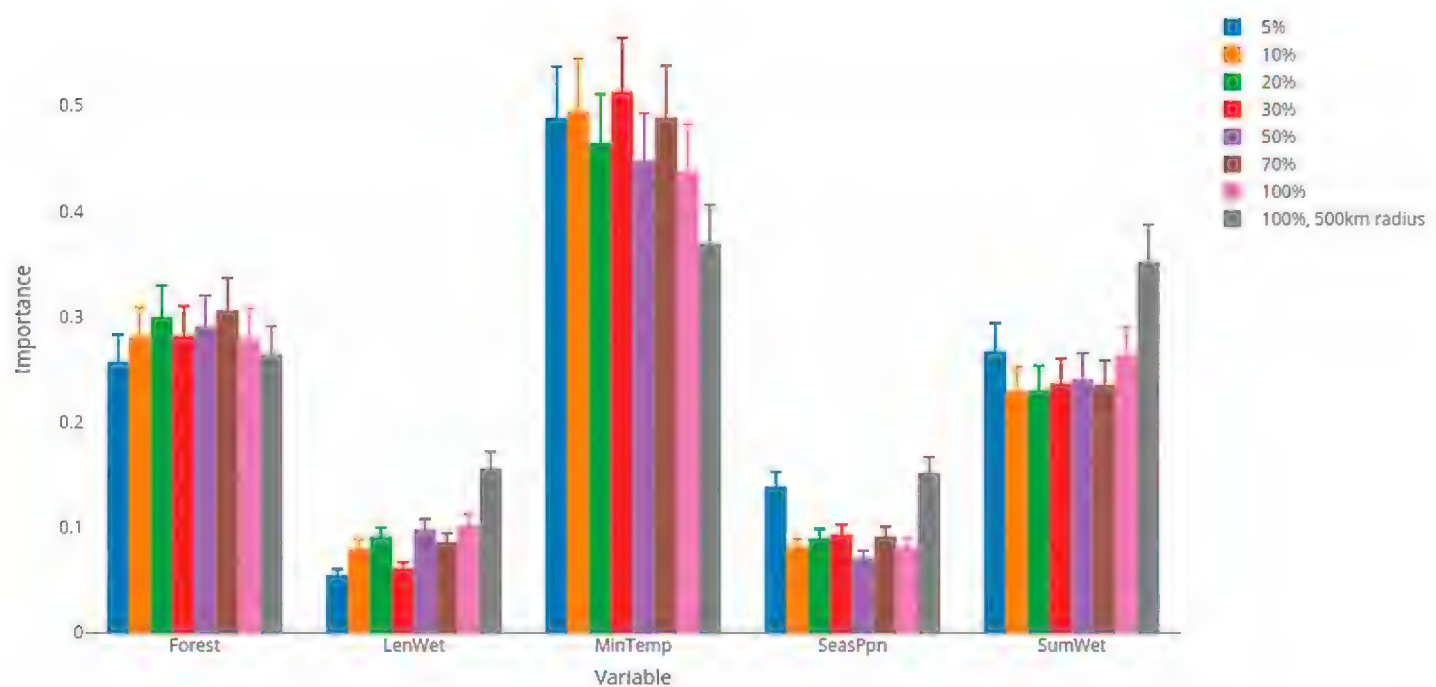
Figure 5. Importance of variables for Species Distribution Models (SDMs) of fall armyworm in the Americas and Africa. Colour codes indicate the percentage of the African distribution that was sub-sampled or the pseudo-absence selection background. Error bars are standard deviations of the results across all SDM techniques and distribution datasets.

China, India Indonesia and, to a lesser extent, Australia and Thailand. Countries vulnerable to fall armyworm (outside South America) that receive the greatest number of passengers embarking from African source countries are Australia, China, India, Indonesia, Malaysia and the Philippines. These countries are likely to be the most imminently threatened by fall armyworm invasion.

Discussion

SDM results were encouragingly accurate and indicated that much of sub-Saharan Africa is highly suitable year-round for fall armyworm, from the Saharan belt to South Africa. Within this region, much of Congo, DRC, Gabon and Cameroon have low suitability (though uncertainty is high in some of these areas). Low suitability in these countries is likely because of extensive forest cover. However, this does not mean that pockets of suitable habitat in those countries will not be severely affected, given the ability of fall armyworm to travel long distances (see below for further discussion of forested areas).

Much of Northwest and Northeast Africa has low suitability (<40% probability of occurrence, Figure 4), so might not host year-round populations of fall armyworm. However, Sudan's and Egypt's Nile Valley may be suitable during wet parts of the year and is adjacent to fall armyworm's likely year-round range in South Sudan and Ethiopia. Fall armyworm's 1700 km annual migration in North America suggests a similar migration could be possible into the Nile Valley, which could threaten maize and cotton production. Indeed, migrating fall armyworm is a severe pest of cotton in the USA (Hardke et al. 2015). Simulations of fall armyworm dispersal from the Khartoum area of Sudan and the Addis Ababa area of Ethiopia confirm this as a strong possibility (Heinrichs et al. 2018).

In currently un-invaded portions of Africa, there are pockets of high suitability in Morocco's productive agricultural regions, as well as the Libyan coast. Transportation to North Africa (countries with part of their land mass north of the Sahara) via trade or air transportation routes from sub-Saharan Africa is less likely than transportation outside Africa (Suppl. material 1: Figure S6). The suitable areas in Morocco are 2,500 km straight-line distance from the year-round distribution. This is far beyond the distance travelled by individuals from a single fall armyworm population in North America and so colonisation directly from the year-round distribution may be unlikely. However, some Lepidoptera are thought to migrate across the Sahara annually (Stefanescu et al. 2016). If fall armyworm were to establish in Morocco, seasonal migrations into Europe would be highly likely. There are pockets of climate suitable for year-round populations (i.e. grid-cells with a suitability value of ≥0.5) in south and northeast Iberia, Italy and Greece.

Low-suitability areas in sub-Saharan Africa may still experience infestation from migrating fall armyworm during some seasons. Nagoshi et al. (2007) suggested that considerable fall armyworm migration within Central and South America occurs in response to seasonal changes in rainfall, temperature and agricultural plantings. This is supported by the notable genetic mixing amongst populations as widely dispersed as Argentina, Mexico and Mississippi (Clark et al. 2007). Migration within Africa would make it very difficult to control fall armyworm outbreaks by managing any single location. Instead management would have to be coordinated across regions and country borders.

Research into seasonal migration and population dynamics within sub-Saharan Africa is clearly needed. Understanding the potential for annual migrations both within and beyond the year-round range requires forecasts of the speed, direction and heights of prevailing wind during periods when fall armyworm populations are large. We also need to know the migration capacity of African fall armyworm populations. The propensity of individuals to migrate and the length of time for which adults can fly varies within populations, often genetically (Roff and Fairbairn 2007). Migration capacity in Africa may differ from that in the putative native range, due to founder effects and selection during introduction. Using flight mills (Minter et al. 2018), Mark Release Recapture and population genetics could elucidate migration capacity. A cellular automata approach could be useful for modelling the spread of seasonal outbreaks (Garcia and Godoy 2017).

Much of South and Southeast Asia and areas of Australia are highly suitable for fall armyworm year-round. Natural dispersal towards this region is considered unlikely, as the distance is over 2000 km, further than fall armyworm is recorded to have travelled in the Americas. Nonetheless, the southwest monsoon blows from Africa to India beginning in June and is a possible route by which fall armyworm adults could arrive in India by their own dispersal. There are important invasion routes from Africa into South and Southeast Asia and Australia (Figure 4). Arrival via imported commodities or passenger air travel is most likely where entry ports are found in environmentally suitable locations for a given pest (Tatem and Hay 2007). Targeted screening and rapid response mechanisms could help reduce the likelihood of arrival and establishment in these locations. However, management efforts should not be confined to individual countries. There are large, spatially cohesive areas of environmentally suitable areas

throughout Asia and Australia (Figure 4a). The rapid spread in Africa suggests that, if fall armyworm reaches one location in Asia or Australia, it could spread throughout the entire region using its own dispersal mechanisms, rather than simply establishing near to the arrival point. Thus, if fall armyworm arrives anywhere in Asia or Australia, rapid cross-border communication and collaboration will be key to effective management.

As conditions outside the predicted year-round range (for example, Europe) might be suitable in certain seasons, improved predictions of seasonal suitability could be achieved with demographic modelling of data from lab or field trials or from statistical modelling (e.g. Tonnang et al. 2011). If demonstrated to be robust, demographic predictions could identify areas where crops eaten by fall armyworm are grown during seasons when migration could occur.

The results of Species Distribution Modelling were encouragingly accurate. AUC values from cross-validation were well within the range usually considered acceptable for SDM studies of invertebrates (Kharouba et al. 2013). This is encouraging given the somewhat uneven recording effort, the likelihood that fall armyworm is under-recorded in the Americas, and the large area for which projections were made. SDM projections were consistent across sub-sampled data. Indeed, areas in Colombia, Panama, Venezuela and Brazil known to harbour fall armyworm, but from which no or few presences were recorded, were predicted to be environmentally suitable (Figure 4). In addition to Ghana and Zambia, fall armyworm's distribution has been well characterised in South Africa. These data were not available to include in models, but visual inspection demonstrates that SDMs seem to predict the extent of fall armyworm's distribution in South Africa as reported in May 2017 (Erasmus 2017). Moreover, the predictions are broadly similar to those obtained from CLIMEX modelling (Du Plessis et al. June 2018). Projections from ensembles using differing data sub-samples did not lead to substantially lower suitability or greatly differing geographic patterns of suitability (Suppl. material 1: Figures S1, S2). This indicates that the intensive surveying in Ghana and Zambia has not caused over-fitting to environmental conditions in those countries.

Forest, MinTemp (coldest annual temperature) and SumWet (rainfall during the wettest three months) were consistently identified as the environmental variables that most affected fall armyworm's distribution. The importance of MinTemp supports the existence of a hard polewards geographical boundary, caused by one or more months where temperature drops below a threshold. This suggests that climate warming could expand the potential range of fall armyworm. SumWet was consistently more important than LenWet (rainy season length) or SeasPpn (the contrast between the rainy and dry seasons). In order to understand if this is due to indirect (i.e. through host plant growth) or direct effects, one could use structural equation modelling incorporating the yield of key host plants, or incorporate life-history parameters from Suppl. material 1: Table S1 into demographic models. The importance of 'Forest' is likely because it indicates the availability of crops on which fall armyworm feeds. This could also suggest that few people have looked for fall armyworm outside of areas with extensive crop coverage. It would be useful to study fall armyworm's survival in forested habitat and in small cropped areas

surrounded by forest. This would inform models of invasion into Congo, DRC, Gabon, and Cameroon, where low projected suitability is likely caused by high forest cover.

Rapid evolution of climate tolerances can occur in pest insects following invasion, i.e. a 'niche shift' (Hill et al. 2013; Hill et al. 2017). Evolutionary niche shifts would compromise invasion forecasts using any modelling technique relying on data from native populations. This includes SDMs (Early and Sax 2014), CLIMEX (Sutherst et al. 2004) and physiological and demographic approaches such as Insect Life Cycle Modeller (Tonnang et al. 2011). In addition to evolution, niche shifts can also occur during invasion due to species' native distributions not occupying all environmentally suitable locations. However, non-evolutionary niche shifts are uncommon in widespread agricultural pests such as fall armyworm (Early and Sax 2014). In any case, niche shift analysis finds that rapid evolution of climate tolerances does not seem to have occurred for the fall armyworm (95% of the studied naturalised range display niche stability, Figure 3). It therefore appears that we can be confident in the accuracy of range forecasts that utilise native distribution data. However, there is still a significant part of the niche unoccupied in Ghana and Zambia that is suitable for the species based on the native range distribution. Thus, it is likely that the species will continue its rapid infilling of its potential African range (Day et al. 2017).

It is interesting to note that fall armyworm was not high on a recent list of pest species likely to invade West Africa (in the lower 50th percentile for Ghana, Nigeria and Togo (Paini et al. 2016, pers. comm. Paini). This list was constructed using a Self-Organising Map (SOM) approach. SOM calculates the relative likelihood a target pest species will establish in a region based on whether pests whose range overlaps the target species have also invaded there. The low establishment index calculated for fall armyworm is likely because few pest species have previously jumped from the Americas to Africa, which in turn is presumably because of historically low trade between the two continents (Cock et al. 2017; Seebens et al. 2015). While the SOM approach is highly valuable, rapidly changing global trade and transportation patterns open invasion routes that pest species rarely travelled in the past (Early et al. 2016; Seebens et al. 2015). Therefore, there may be many other inter-continental pest invasions that are hard to predict.

Very little research has been done into differing climate tolerances between maize and rice strains and there is insufficient information on their respective distributions to apply SDMs to each strain (see Methods). Slight differences in basal temperatures of the two strains result in approximately one more generation of the rice strain per year at the optimum temperature of 25 °C, i.e. 12 generations (Busato et al. 2005). The two strains appear to have substantially overlapping ranges, so any difference in tolerances is likely not to affect the geographic range greatly, but could affect abundance and impact. The African maize strain population appears to have passed through a genetic bottleneck (Abrahams et al. 2017). The population may thus have slightly more restricted climate tolerances than the species as a whole and environmental suitability worldwide may be overestimated. However, fall armyworm's widely observed distribution in Africa suggests any overestimation is slight. The predominance of the maize strain in Africa may influence the establishment of

fall armyworm from Africa in environmentally suitable parts of Asia, where rice is much more widely grown than maize.

Diet can affect temperature tolerances, and indeed the temperature threshold for development was several degrees lower when fall armyworms were fed leaves from early vegetative maize plants than when fed leaves from late vegetative or reproductive plants (Barfield and Ashley 1987) (Suppl. material 1: Table S1). Environmental conditions can alter the impacts of biopesticides and infection rates of diseases and natural enemies that control pests, including in fall armyworm (Elderd and Reilly 2014; Murúa et al. 2006; Tonnang et al. 2017). Predictions of range, abundance, impacts and the outcomes of Integrated Pest Management strategies would therefore benefit from a better understanding of the relationship between strains, diet, pesticide effectiveness and environmental limits on distributions. Given the encouragingly robust results of SDMs based on climate and land use variables, future work could extend statistical modelling to the relationship between environmental suitability and fall armyworm abundance and impact on crops. If data on the distribution of potential biocontrol agents could be obtained, their environmental suitability for these species could be also studied using SDMs.

Given the likely onward spread of fall armyworm, a united international response is clearly needed and is indeed emerging. In Africa, the Food and Agriculture Organization of the United Nations is coordinating responses to fall armyworm, providing support for early warning tools, farmer field schools on integrated pest management, and a food security risk assessment model. A research consortium uniting Africa and Asia has recently been launched. Led by CGIAR, the Fall Armyworm R4D consortium aims to develop integrated pest management solutions including host plant resistance, environmentally safer chemical pesticides, biological and cultural control methods and agronomic management.

Conclusion

The accuracy of SDM results and the similarity of the environments occupied in the native and invaded range support the robustness of the SDM approach. Temperature of the coldest month and the amount of rain during the rainy season are the most important climatic limits of fall armyworm's year-round distribution. Much of sub-Saharan Africa can host year-round fall armyworm populations and seasonal migrations are likely to take place along the Nile into Northeast Africa. The likelihood of seasonal migrations beyond this range seems to be low. South and Southeast Asia and Australia, are highly suitable for fall armyworm. Trade and passenger air travel routes indicate parts of this region into which African populations are particularly likely to be transported. There is therefore considerable potential for near global invasion and seasonal migration of fall armyworm. Vigilance is needed to monitor for the onward invasion of fall armyworm via potential migration routes into North Africa and South Asia and on some high-risk trade and air travel routes. Management decisions would be improved by further research on fall armyworm's seasonal migration and population dynamics and the environmental dependency of interactions with other species.

Acknowledgements

Author contributions

RE conceived the study, collected data, performed analysis and drafted the paper. PG and SM contributed to the acquisition and interpretation of data for the project and revised the manuscript.

Data availability statement

Some distribution data from South America analysed during this study are included in the Supplementary Information files. This does not include data from Plantwise clinics in Bolivia, Honduras, Nicaragua and Peru, due to data sharing restrictions. Some other distribution data are available from CABI's Plantwise programme but restrictions apply to the availability of these data, which were used under licence for the current study and so are not publicly available. Data may be available from the authors upon reasonable request and with permission of Plantwise. All other data used are publicly available from the referenced data sources.

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Supplementary material 1

Supplementary material

Authors: Regan Early, Pablo González-Moreno, Sean T. Murphy, Roger Day

Data type: supplementary results

Explanation note: Table S1. Summary of evidence for fall armyworm developmental and population responses to the environment extracted from literature sources. Figure S1. Effect of different sub-sampling proportions and pseudo-absence selection diameters on model predictions (maps). Figure S2. Effect of different sub-sampling proportions and pseudo-absence selection diameters on Balanced Accuracy. Figure S3. Histograms of each environmental variable in 10 arc-minute grid-cells from which the fall armyworm is recorded. Figure S4. Multivariate Environmental Similarity Surface analysis. Figure S5. Empirically measured environmental effects on fall armyworm life cycle. Figure S6. Trade and passenger air transportation within Africa.

Link: https://doi.org/10.3897/neobiota.40.28165.suppl1

Supplementary material 2

Table S2. Distribution data from the Americas

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Data type: occurrence

Link: https://doi.org/10.3897/neobiota.40.28165.suppl2